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When molecules claim for taxonomic changes: New proposals on the classification of Old World treefrogs

(Amphibia, Anura, Ranoidea)

Miguel Vences & Frank Glaw

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Recent phylogenetic data, mainly based on mitochondrial DNA analyses, indicate that current classification of neobatrachian anurans is in need of revision. In the present paper, we review the literature pertaining the molecular and morphological phylogeny of Old World treefrogs. The molecular phylogenies indicate that, among non-hyperoliid Old World treefrogs, one clade is formed by the endemic genera from Madagascar, and a second one by the Asian and African genera. Both these lineages are nested within the family Ranidae sensu Blommers-Schlösser (1993), but their relationships to each other are not unambigously resolved. We propose to consider the Asian-African lineage as family Rhacophoridae and the Malagasy lineage as family Mantellidae. Together with the (paraphyletic) family Ranidae, these two families form the epifamily Ranoidae. Three epifamilies (Arthroleptoidae, Microhyloidae, and Ranoidae) form the superfamily Ranoidea. Within the family Mantellidae, three subfamilies are recognized: Mantellinae (genera *Mantella* and *Mantidactylus*), Boophinae new subfamily (genus *Boophis*), and Laliostominae new subfamily (genera *Laliostoma* and *Aglyptodactylus*). The new classification accounts better for the evolutionary relationships of ranoid frogs and furthermore allows for a classification of the involved Malagasy groups in agreement with their phylogeny. A satisfactory classification of the whole group, however, will only be possible with increased phylogenetic knowledge, and will probably include a further partition of the Ranidae.

Miguel Vences, Muséum national d'Histoire naturelle, Laboratoire des Reptiles et Amphibiens, 25 Rue Cuvier, 75005 Paris, France; address for correspondence: Zoologisches Forschungsinstitut und Museum A. Koenig, Adenauerallee 160, 53113 Bonn, Germany, e-mail m.vences@t-online.de

Frank Glaw, Zoologische Staatssammlung, Münchhausenstr. 21, D-81247 München, Germany, e-mail Frank.Glaw@zsm.mwn.de

1. Introduction

The phylogenetic relationships of Old World treefrogs have been subject of intensive debate during the past decades. First all classified in a family Polypedatidae (e. g. Ahl 1931, Noble 1931, as opposed to the unrelated treefrog family Hylidae with a largely Neotropical distribution), Laurent (1951) noted that one group, which he defined as Hyperoliidae, was osteologically very different from the remaining taxa (placed into the Rhacophoridae or Rhacophorinae). The important differences between these two groups were emphasized later in the phylogenetic approaches of Liem (1970), Drewes (1984) and Channing (1989). However, Laurent (1951, 1986) also noted that, while hyperoliids share several

symplesiomorphies with some African genera formerly considered as basal representatives of the Ranidae (and today seen as own families, Arthroleptidae and Astylosternidae; see Dubois 1992), rhacophorines shared synapomorphies with more derived representatives of the extremely diverse and speciose family Ranidae. Actually, rhacophorids are only distinguished from other ranids by the presence of an intercalary element between ultimate and penultimate phalanges of fingers and toes, and by generally (but not consistently) more arboreal habits. Based on the synapomorphies identified (e.g., presence of a bony sternal style), Laurent (1986), Dubois (1992) and Blommers-Schlösser (1993) proposed to include the Rhacophoridae as subfamily Rhacophorinae in the family Ranidae. However, the proposal of Blommers-Schlösser (1993) (i. e. the definition of the family Ranidae as group containing almost all ranoid taxa with an ossified sternal style) is all but generally accepted by herpetologists. Most authors continue considering the Rhacophoridae as separate family (e.g., Frost 1985), a view also shared by internet databases (as the Amphibian Species of the World database, Amphibiaweb, Tree of life, Genbank; as of 10 November 2000). Furthermore, new names such as "fanged frogs" (Emerson & Ward 1998, Emerson et al. 2000a) and "boophids" (Richards et al. 2000) have been used to address ranoid subclades, without a nomenclatural formalization of these groups.

In the last few years, numerous new results on Old World treefrog phylogeny have been published, several of them referring to the taxa endemic to Madagascar. In the present paper, we will outline the main conclusions that can be drawn from a comprehensive view of the new results, and propose a partly modified classification which better reflects the phylogenetic relationships among ranoid frogs than the previous schemes. We here focus on only a small subset of this speciose group, namely the non-hyperoliid Old World treefrogs (Rhacophorinae and Mantellinae sensu Blommers-Schlösser 1993). Further classificatory modifications will successively become necessary with the accumulation of new data on ranoid groups such as the Hyperoliidae and the Microhylidae.

2. Summary of recently published molecular data on Old World treefrogs

DNA sequences of ranoid frogs have been analyzed in the context of higher-level phylogenies by Hillis et al. (1993), Hedges & Maxson (1993), Hay et al. (1995), Ruvinsky & Maxson (1996), and Vences et al. (2000a). More particular aspects were studied by Bossuyt & Milinkovitch (2000), Emerson & Ward (1998), Emerson et al. (2000a,b), Feller & Hedges (1998), Marmayou et al. (2000), Richards & Moore (1996, 1998), Richards et al. (2000), and Vences et al. (2000b,c). The dissertation of Vences (1999) contains a number of crucial results which are partly published (Vences et al. 2000a,b,c) or in progress of publication (Vences et al. submitted). Wilkinson & Drewes (2000) furthermore undertook a re-analysis of non-molecular characters of Old World treefrogs. Altogether, the new data allowed for the identification of a number of well-supported monophyletic goups, while other splits were much less clearly resolved (compare Fig. 1):

1. Within the derived and monophyletic group of the Neobatrachia (sensu Feller & Hedges 1998), one clade containing exclusively groups with a firmisternal shoulder girdle is identified as monophyletic by all available molecular data (Hillis et al. 1993, Maxson et al. 1993, Hay et al. 1995, Ruvinsky & Maxson 1996, Emerson et al. 2000a, Vences et al. 2000a). This clade includes the Ranidae (with Rhacophorinae and Mantellinae), Microhylidae, Hemisotidae, Hyperoliidae, Arthroleptidae, and Astylosternidae. It does not include several other Neobatrachian groups which apparently evolved a firmisternal or pseudofirmisternal shoulder girdle independently: some leptodactylids, "atelopodine" bufonids, sooglossids and dendrobatids (Duellman & Trueb 1986, Hay et al. 1995, Ruvinsky & Maxson 1996, Graybeal 1997, Vences et al. 2000a).
2. Within the firmisternal clade as defined above, one basal radiation led to the differentiation of the families Microhylidae, Hemisotidae, Hyperoliidae, Arthroleptidae, Astylosternidae, and Ranidae (sensu Blommers-Schlösser 1993). Relationships between all these families are not well resolved, and some (especially Microhylidae and Hyperoliidae) may not be monophyletic (e.g. Emerson et al. 2000a). However, one group containing all or most forms characterized by a bony style of the sternum (Ranidae sensu Blommers-Schlösser 1993, including Rhacophorinae and Mantellinae) appeared as rather well supported monophyletic group in Emerson et al. (2000a) and Vences (1999).
3. A second large and probably explosive radiation led to the differentiation of the more than 980 species in 54 genera (Glaw et al. 1998a) included in the Ranidae sensu Blommers-Schlösser (1993). Again, relationships between the different clades of this radiation can not yet be unequivocally

resolved (Emerson et al. 2000b, Vences et al. 2000c). However, two treefrog clades are well defined by molecular synapomorphies:

- A clade endemic to the Madagascan region which is composed of the genera *Boophis* (Rhacophorinae), *Mantella* and *Mantidactylus* (Mantellinae), *Laliostoma* (formerly *Tomopterna;* Raninae) and *Aglyptodactylus* (Rhacophorinae, Mantellinae or Raninae) (Richards & Moore 1998, Glaw et al. 1998b, Richards et al. 2000, Bossuyt & Milinkovitch 2000, Vences et al. 2000b, Vences et al. submitted).
- A clade with representatives in Africa and Asia which contains the genera classified in the Rhacophorinae except the Malagasy *Boophis* (Richards & Moore 1998, Emerson et al. 2000a, Richards et al. 2000, Vences et al. submitted).

3. Problems in the classification of Malagasy ranoids

The endemic, non-hyperoliid and non-microhylid ranoid frogs endemic to the Madagascan region have generally been classified in three subfamilies or families (Frost 1985; Blommers-Schlösser & Blanc 1991; Duellman 1993). The phylogenetic results outlined above show that none of the discussed classifications is fully satisfactory.

- *Laliostoma labrosum* was included in the genus *Tomopterna* and the subfamily Raninae or Tomopterninae until recently (Dubois 1992, Glaw et al. 1998b). Molecular studies of Vences et al. (2000b) revealed that the three geographic groups of *Tomopterna* (Africa, Madagascar, southern Asia) are not closely related (see also Bossuyt & Milinkovitch 2000), and should be included in different genera – *Laliostoma* being the monotypic Malagasy genus. Richards & Moore (1998) found that *Mantidactylus, Mantella, Boophis, Aglyptodactylus* and *Laliostoma labrosum* are a monophyletic clade, and suggested that the latter is a rhacophorid. *Laliostoma* is the only endemic ranoid from Madagascar without an intercalary element.
- *Aglyptodactylus* has mostly been considered as belonging to the Rhacophorinae (Blommers-Schlösser 1993), but has sometimes also been included in the Mantellinae (Channing 1989). Glaw et al. (1998b) found that *Aglyptodactylus* and *Laliostoma labrosum* are closely related based on non-molecular characters although both were traditionally classified in different subfamilies. To remove this classificatory inconsistency they transferred *Aglyptodactylus* to the Raninae. Extended data sets of non-molecular characters (Vences et al. in prep.) and molecular data (Vences et al. 2000b and submitted) confirm close relationships of *Aglyptodactylus* and *Laliostoma.*
- The genera *Mantella* and *Mantidactylus* form the subfamily Mantellinae (a third taxon, *Laurentomantis*, is considered as one out of 12 subgenera of *Mantidactylus*; Glaw & Vences 1994). This clade is well defined by ethological synapomorphies (reduction of strong mating amplexus; egg deposition outside of water). The Mantellinae were either included in the Rhacophoridae (Channing 1989) or Ranidae (Frost 1985, Blommers-Schlösser 1993, Glaw et al. 1998b), or seen as own family Mantellidae (Blommers-Schlösser & Blanc 1991, Dubois 1992).
- The genus *Boophis* has generally been included in the rhacophorines which are either considered as subfamily Rhacophorinae of the Ranidae (e.g. Blommers-Schlösser 1993) or as family Rhacophoridae (e.g. Frost 1985).

4. A new classificatory scheme of the superfamily Ranoidea

The data summarized above clearly corroborate Duellman & Trueb's (1986) statement that ranid systematics are "in a state of chaos" and demonstrate the need of an update of the classificatory scheme. The molecular data indicated the presence of multiple para- and polyphyletic taxonomic units within ranid frogs (e.g. Emerson et al. 2000a, Vences et al. 2000b). The main goal to be achieved in ranid systematics in the near future is, in our opinion, a classification void of polyphyletic taxa, and without or with only a small number of paraphyletic taxa.

Several authors have followed a strategy to exclude small, well corroborated monophyletic groups from large catch-all groups, as a first contribution to a partition of these large groups into monophyletic units (e.g. Drewes 1985). We here consider the same approach as useful for the case of the family

Ranidae which is large and diverse enough to be partitioned into several families. Largely based on the scheme of Dubois (1992), we propose:

- to consider the taxa joined in the Ranidae by Blommers-Schlösser (1993) as epifamily (sensu Dubois 1992) Ranoidae.
- to join the families Arthroleptidae, Astylosternidae and Hyperoliidae in an epifamily Arthroleptoidae, and the families Hemisotidae and Microhylidae in an epifamily Microhyloidae. The monophyly of the Ranoidae appears rather well assessed, while the monophyly of the remaining two epifamilies is questionable at current state (but not contradicted by any relevant data sets).
- to recognize, within the Ranoidae, a family Rhacophoridae beside the Ranidae. This family Rhacophoridae contains the Asian and African rhacophorine genera but not the Malagasy *Boophis*.
- to recognize, within the Ranoidae and beside the Ranidae and the Rhacophoridae, a family Mantellidae, which contains the endemic Malagasy genera *Mantella, Mantidactylus, Boophis, Aglyptodactylus* and *Laliostoma*.
- to subdivide the Mantellidae into the following three subfamilies which correspond to three monophyletic groups (Richards & Moore 1998, Bossuyt & Milinkovitch 2000, Richards et al. 2000, Vences et al. 2000b):

1. Mantellinae Laurent, 1946
Type genus *Mantella* Boulenger, 1882.
Genera: *Mantella* Boulenger, 1882 and *Mantidactylus* Boulenger, 1895.
Distribution: Madagascar and Mayotte Island.

Arboreal, scansoriel, terrestrial or semi-aquatic firmisternal frogs with a bony sternal style and an intercalary element between ultimate and penultimate phalanges of fingers and toes. Almost all species with three free tarsal elements, although the third element may be very small in many species and absent in rare cases. Finger and toe pads with a complete circummarginal groove. First finger shorter or of similar length as second finger. Males without nuptial pads, and mostly with femoral glands. Derived reproductive biology (absence of strong mating amplexus, egg deposition outside of water).

2. Boophinae, new subfamily
Type genus *Boophis* Tschudi, 1838.
Genus: *Boophis* Tschudi, 1838.
Distribution: Madagascar and Mayotte Island.

Arboreal (some species partly terrestrial) firmisternal frogs with a bony sternal style and an intercalary element between ultimate and penultimate phalanges of fingers and toes. Two or three free tarsal elements. Finger and toe pads with a complete circummarginal groove. First finger shorter or of similar length as second finger. Males with nuptial pads but without femoral glands. Generalized reproductive behaviour; eggs (no foam nests) are laid into free water (not in leaf axils nor treeholes).

3. Laliostominae, new subfamily
Type genus *Laliostoma* Glaw, Vences & Böhme, 1998.
Genera: *Laliostoma* Glaw, Vences & Böhme, 1998 and *Aglyptodactylus* Boulenger, 1919.
Distribution: Madagascar.

Terrestrial firmisternal frogs with a bony sternal style and with *(Aglyptodactylus)* or without *(Laliostoma)* intercalary element between ultimate and penultimate phalanges of fingers and toes. Two free tarsal elements. Finger and toe pads without a circummarginal groove. First finger distincly longer than second finger. Males with blackish nuptial pads (when breeding) but without femoral glands. Generalized reproductive behaviour; eggs are laid into free stagnant water.

5. Discussion

The new classification proposed (Tab. 1, Fig. 1) divides the "ranids" sensu Blommers-Schlösser (1993) into a number of well-defined monophyletic taxa, and one paraphyletic taxon. The epifamily Ranoidae corresponds to the monophyletic clade of ranoid frogs morphologically defined by an ossified sternal style (secondarily reduced in a few taxa). This epifamily consists, according to our classification, of three families: the monophyletic Rhacophoridae and Mantellidae as defined here, and the paraphyletic Ranidae. The latter group will certainly be subject of further partitioning in the future; for example, the African groups defined as Cacosterninae by Blommers-Schlösser (1993) (possibly together with the genus *Tomopterna;* Vences et al. in 2000b), and the Petropedetinae, which probably merit recognition at familial level. The same is true for the enigmatic genera *Ptychadena, Hildebrandtia* and *Lanzarana* (Ptychadeninae sensu Dubois 1992).

Within the Mantellidae, three further monophyletic groups are recognized according to our classification. These groups are considered as subfamilies. The advantage of this treatment is that the well-established definition of Mantellinae as a group containing the genera *Mantella* and *Mantidactylus* (e.g. Blommers-Schlösser 1993, Glaw & Vences 1994) remains stable. The classification of the five genera *(Aglyptodactylus, Boophis, Laliostoma, Mantella, Mantidactylus)* in three subfamilies (Boophinae, Laliostominae, Mantellinae) of one family replaces their former classification in three subfamilies (Rhacophorinae, Raninae, Mantellinae) of two or three families. The proposed classification is therefore no exaggerated splitting approach. In addition, it must be kept in mind that two of the involved genera are very speciose: *Mantidactylus* currently contains about 70 nominal species in 12 subgenera, and *Boophis* contains more than 40 species in seven species groups. At least 15 new species of each genus are currently in progress of description. *Mantidactylus* is furthermore paraphyletic (Richards et al. 2000) and very diverse regarding the morphology, ecology, and reproductive biology of the species included. We expect that both genera will be partitioned at genus level when phylogenetic information becomes available to characterize sufficiently the respective lineages.

In a purely cladistic sense, the proposed classification introduces paraphyly into ranid classification (by accepting a paraphyletic Ranidae beside the Mantellidae and the Rhacophoridae). However, this situation is already implicitely accepted by recognition of the Rhacophoridae at family level, by the majority of herpetologists. Furthermore, we consider this paraphyly as a transitory stage, to be

Tab 1. Summary of the ranoid classification of Dubois (1992) and the proposed modifications according to new phylogenetic data (M monophyletic, P paraphyletic according to present state of knowledge). Subfamilies are only shown for the Malagasy family Mantellidae.

Classification according to Dubois (1992)	Proposed classification
Superfamily Ranoidea	Superfamily Ranoidea (M)
Epifamily Arthroleptoidae	Epifamily Arthroleptoidae (M?)
Family Arthroleptidae	Family Arthroleptidae (M)
Family Astylosternidae	Family Astylosternidae (M?)
Family Hyperoliidae	Family Hyperoliidae (P?)
Epifamily Dendrobatoidae	
Epifamily Hemisotoidae	Epifamily Microhyloidae (M?)
Family Hemisotidae	Family Hemisotidae (M)
Epifamily Microhyloidae	Family Microhylidae (M?)
Family Microhylidae	
Family Scaphiophrynidae	
Epifamily Ranoidae	Epifamily Ranoidae (M)
Family Mantellidae	Family Ranidae (P)
Family Phrynobatrachidae	Family Rhacophoridae (M)
Family Ranidae	Family Mantellidae (M)
[Subfamily Rhacophorinae]	Subfamily Mantellinae (M)
[Subfamily Tomopterninae]	Subfamily Boophinae (M)
[Subfamily Raninae]	Subfamily Laliostominae (M)

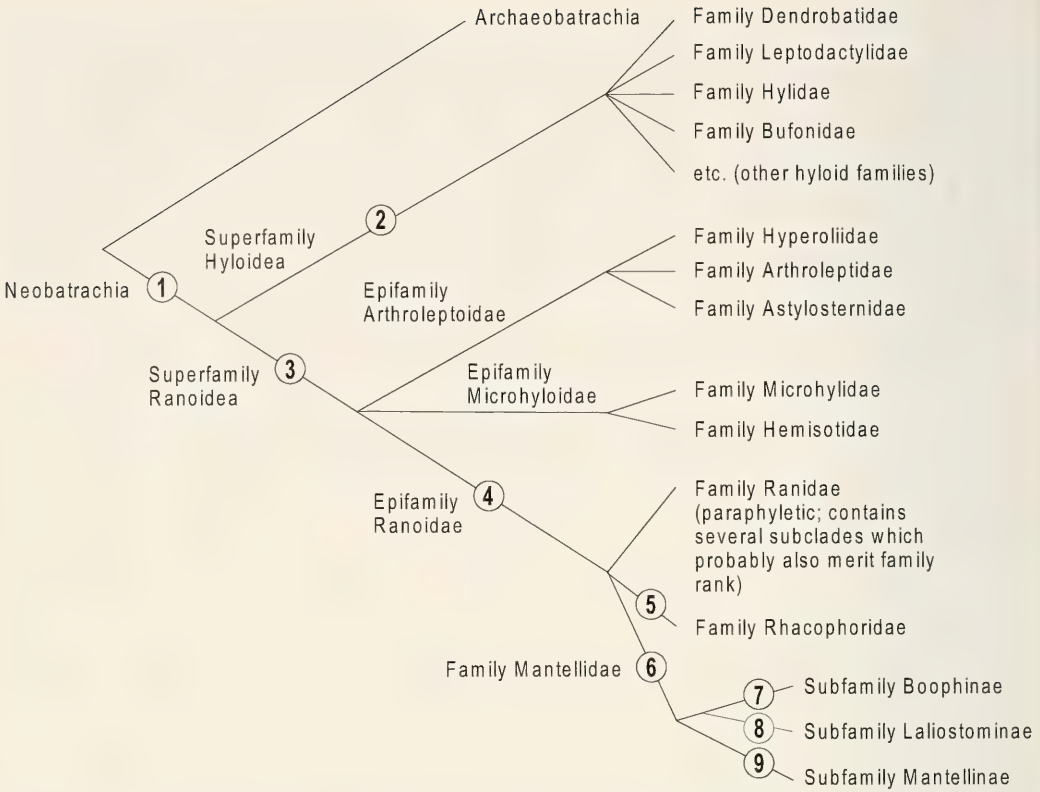

Fig. 1. Schematic phylogenetic consensus tree based on recently published molecular data, clade names according to proposed scheme. Only selected groups are included in the figure; subfamilies are only shown for the family Mantellidae. Evidence for the monophyly of numbered clades is, respectively, provided in the papers of (1) Hay et al. (1995), Feller & Hedges (1998); (2) Hay et al. (1995), Ruvinsky & Maxson (1997), Feller & Hedges (1998), Vences et al. (2000a); (3) Hay et al. (1995), Feller & Hedges (1998), Vences et al. (2000a), Emerson et al. (2000a); (4) Emerson et al. (2000a), Marmayou et al. (2000), Vences et al. (2000c), Vences et al. (submitted); (5) Richards & Moore (1998), Bossuyt & Milinkovitch (2000), Richards et al. (2000), Vences et al. (submitted); (6) Richards & Moore (1998), Bossuyt & Milinkovitch (2000), Richards et al. (2000), Vences et al. (2000b); (7) Richards & Moore (1998), Bossuyt & Milinkovitch (2000), Richards et al. (2000), Vences et al. (2000b); (8) Glaw et al. (1998b), Richards & Moore (1998), Richards et al. (2000); (9) Bossuyt & Milinkovitch (2000), Vences et al. (2000b).

maintained only until more ranid clades of unquestionable monophyly are identified and considered as distinct enough to merit familial rank.

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